THE EFFECTS OF ILLUMINATION ON RESPONSES TO ELECTRICAL STIMULATION IN *MIMOSA PUDICA* L.

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Tom Norman Hooe

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Approved by Committee:

Chairman

Dean of the School of Graduate Studies

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INTRODUCTION AND REVIEW

The study of light and touch stimulated responses in plants offers a convenient system for investigating the physiology of plant movements. Mimosa pudica has well-known leaf movement reactions that exhibit responsiveness to both light and seismic stimuli. The organ of response to both stimuli is the pulvinus. Transmission of the stimulus to the pulvinus is accomplished by the generation of an action potential in phloem tissue (Sibaoka, 1969). This current investigation has been designed to detect a relation between light and shock stimuli by measurement of the velocity of action potentials, at selected times in the photoperiod.

Like many legumes, M. pudica has a sleep movement pattern that has been thoroughly studied. The evolutionary significance of nyctinastic movements may be debated, but it has been shown that the vertical position of leaves at night increases resistance to cold (Darwin, 1881). M. pudica also has the capabilities of receiving, conducting and responding to other stimuli not related to photoperiod. The mode of transmission of the stimuli has been debated but in all cases it has been related to the vascular tissue. The form of the transmitted impulse is probably electrochemical in nature. Upon receiving the impulse the pulvinus loses turgidity allowing the leaf to droop. Recently, phytochrome has been suggested as a factor controlling M. pudica responsiveness.

Stimulation may be applied to M. pudica in a variety of ways. Hug (1964) used x-ray induction and detected electrical potentials traveling in the petiole with a mean velocity of 15 mm./sec. The drooping of the leaf at the primary pulvinus follows photostimulation if the pulvinus is illuminated after being held in darkness (Fondeville et al, 1967). Stimulation has also been accomplished with ethyl ether, flame, scratching, and ice. In each case similar responses were recorded (Aimi, 1963 and Bose, 1913a). Stimulation by a low voltage DC current is easily quantitied. Bose (1913b) found that a 5-12 volt DC shock would stimulate the pulvinus, but greater voltages caused the plant to become insensitive. Transmission velocities in the petiole varied between 8 and 25 mm./sec.

The mode of transmission of the stimulus to the point of action, the pulvinus, has been debated. The transpiration stream was initially considered as the prime mode of transmission of the stimulus. This was tested by using eosin stain to measure the velocity of solute movement. This velocity was compared to known conduction velocities in M. pudica (Ricca, 1926). A correlation was shown but did not account for the fast conduction responsible for the motile action (Snow, 1924).

Another mode of conduction was suggested involving the release and movement of some type of hormone (Ball, 1927). This method of conduction in the vascular tissue also fails

to account for the speed of transmission. It was believed that a hormone set free from the pith upon stimulation was either transmitted or successively stimulated cells in the vascular tissue.

A third theory on the conduction of the generated impulse was one that completely discounted both the hormonal and transpiration current methods. The generation of an electrochemical action potential along the phloem tissue accounted for transmission at a velocity known to exist in M. pudica. This method of transmission would also allow conduction in both acropetal and basipetal directions (Bose, 1926). The impulse had a mean velocity of 15-16 mm./sec., which is much faster than the slow movement of sap against the transpiration current (Molisch, 1929). Dutt and Guhathakurta (1962) were able to support the electrochemical method of transmission and suggested that the biphasic impulse was initiated by the hydrostatic impact of the pulvinus. Velocities ranging from 10-80 mm./sec. indicated that there was great variability in the transmission of the impulse.

Sibaoka (1953) found two types of conduction in M. pudica petioles. After inserting electric probes into the phloem, he measured resting potentials of approximately -120 mv. When stimulated, these cells generated action potentials with velocities of 20-30 mm./sec. Sibaoka referred to these waves as M waves. Other impulses were also detected with -50 mv. resting potentials and velocities of 2-6 mm./sec. These he

called S waves. Velocities in the petiole were found to approximate the M wave type while in the pulvinus the conduction appeared to be of the S wave type. Conduction in a basipetal direction appears to be of the M wave type until it reaches the pulvinus where it slows down to the velocity of an S wave. Upon crossing the pulvinar junction, the velocity returns to the M wave type (Sibaoka, 1969). Action potentials show "all or none" characteristics and differential conduction velocities exist in the acropetal and basipetal directions. Basipetal velocities always slightly exceeded acropetal (Sibaoka, 1969).

It has been suggested that differences in the resting potentials of phloem cells of M. pudica are established by sodium pumps. These pumps are thought to operate in the tonoplast and plasmalemma creating potentials of -100 to -150 mv. (Dainty, 1962).

By inserting probes into the phloem and protoxylem cells, Sibaoka (1962) found a resting potential of approximately -160 mv. In other cells surrounding these tissues he found resting potentials of -50 mv. Membrane action potentials were always developed when stimulating electrodes were located in -160 mv. resting potential cells while cells with the lower resting potential only developed slight change (Sibaoka, 1962).

The pulvinus in M. pudica is an area of specialized tissue capable of varying its turgor pressure (Weintraub,

1950). Pulvini are found in many plants and in M. pudica these structures are localized at the base of the petiole, the junction of the rachises and also the junction of pinnule pairs. The motile action is thought to result from antagonistic action of the upper and lower halves of the pulvinar region (Asprey and Palmer, 1955). However, investigations have shown that movement would continue to occur if the upper or lower halves of the pulvinus is removed. Excising the lower half will allow the leaf to fall but not return, while excising the upper half, the leaf will fall and return sometimes to an even higher position (Palladin, 1926). It was also found that the greatest electrochemical change occurs in the lower part of the pulvinus (Sibaoka, 1951). It is stated by Weintraub (1950), however, that the upper half is of greater sensitivity and thus accounts for the movement.

The pulvinus is affected by many environmental factors that also affect other aspects of M. pudica sensitivity. Temperature was found to affect the action of the pulvinus while relative humidity seemed to have little effect. The speed of action of the pulvinus increased as a function of temperature increase to an optimum near 40°C. (Wallace, 1931). The pulvinus was also found to be most sensitive in the early morning hours around 5 a.m., and least sensitive between the hours of 1-7 p.m. (Wallace, 1931).

The action of the pulvinus is due to an increased permeability of the membranes of its parenchymal cells (Sen,

1922). The action takes a measurable amount of time, varying from 1/10 to 1/20 of a second for a latent period (Dutt and Guhathakurta, 1962). Some of the most interesting work with pulvinar action in M. pudica was accomplished by observing tannin vacuoles in the pulvinar cells. These were originally thought to be vacuoles within the larger central vacuole of the parenchyma cell. Treatments with tannin solvents have, however, indicated that the tannin is a dense mass in the larger central vacuole not included in its own membrane (Datta, 1957).

The tannin masses decrease in size as the pulvinus reacts to a stimulus, and liquids high in potassium ions are released to the intercellular spaces. This decrease in size of the tannin masses as the pulvinus reacts indicates their role in the motile action (Dutt, 1957).

The action of active transport systems involves the expenditure of energy. It was observed that ATP levels in the pulvinar regions were reduced by 30 to 40 per cent upon stimulation and resultant leaf drop (Liubimova, 1964). This would tend to indicate that energy is utilized for leaf dropping predominately at the time of action.

An organized method of transport must be present if electrochemical gradients are developed along the petiole. Conduction channels of the action potential have been shown to coincide with the phloem. The continuity of the phloem and protoxylem tissue and the capability for forming reflex

arcs at the terminal ends of the rachis tends to substantiate this idea (Bose and Saha, 1967). The petiole of M. pudica has four leaf traces located in the four quadrants of the petiole. Each bundle extends into one of the four rachises. The individual bundles are responsible for carrying the impulse to each respective rachis (Bose and Saha, 1967).

Elements of the phloem tissue in the vascular bundles of M. pudica have been shown to be of two types (Kundu and Saha, 1967). M. pudica is an atypical angiosperm in this respect, because it possesses both nucleated and enucleated mature sieve tube elements. Larger enucleate sieve tubes tend to have a resting potential of around -50 mv. and appear to function mainly in movement of solutes in the plant. Narrow nucleated sieve tubes that have a resting potential of -160 mv. seem to function primarily in the transport of the action potential developed (Kundu and Saha, 1967). This histological work appears to substantiate the ideas presented by Sibaoka in his measurements of resting potentials.

The action of light as the prime stimulating source, has caused this particular sleep action to follow an exogenous pattern. Phytochrome has been indicated as an agent which enhances leaf closure as it accumulates in the far-red form with exposure to red or white light. Leaf closure times at onset of darkness were found to be shortest if the dark period began following a long light period (Hillman and Koukhari, 1967). Phytochrome appears to be concentrated in the tips of

pinnule pairs and the pinnules appear to act locally having no effect on other portions of the leaf (Koukhari and Hillman, 1968). The closing reaction of the pinnules has been shown to be enhanced by phytochrome in the far-red absorbing form with the response expressed in approximately thirty minutes (Burkholder and Pratt, 1936; Fondeville, Borthwick and Hendricks, 1966).

MATERIALS AND METHODS

Plants of M. pudica were grown from seed in a twelve-twelve photoperiod in four inch soil-filled pots. The soil was maintained in a moist condition, and 15-15-15 HELLER-GRO plant food was added every two weeks. Upon reaching a height of eight to twelve inches the plants were placed in a Percival Growth Chamber (Model E-54U) with a twelve-twelve photoperiod. Placing the plants at a mean distance of twelve inches allowed an illumination of fifteen hundred foot-candles from a light source of incandescent and florescent lamps. Temperatures in the chamber were initially regulated to a 29°C. value during the day and 18°C. value at night. Since the action potential developed is temperature dependent, data were also acquired with a constant day-night temperature of 24°C. Temperature has been shown to increase the velocity of impulse transmission in the petiole of M. pudica (Bose, 1913a).

Leaves, third from the apex of healthy plants, were selected for all observations due to their high state of

physiological activity (Dutt, 1962). Leaves were left intact on the plant through all stages of preparation and data collection.

Electrodes were constructed by soldering 5 cm. pieces of 34 gauge stainless steel wire to 1 m lengths of 40 gauge copper wire. The steel ends of the electrodes were inserted through the epidermis from the dorsal groove through the dorsal and lateral surface of the petiole. Insertion is best accomplished by supporting the petiole with the index finger and piercing the tissue with the stainless electrode. Insertion was accomplished 6 hours prior to data collection and care was taken not to damage underlying conductive tissues. A drop of non-nutrient agar placed on the point of insertion will maintain the electrode in a workable condition for up to three to four days. Two electrodes were inserted in the petiole for electrical stimulation approximately 5 mm. apart and about 10 mm. from the junction of the rachises. Electrodes for data collection were inserted in the petiole approximately 5 mm. and 25 mm. respectively from the node.

The plants were stimulated by connecting the two distal electrodes to a Grass Stimulator. A nine volt square wave DC shock stimulus was applied to the petiole of each leaf for 1/5 second. This method of treatment was used in all data collected.

The action potential developed was recorded by connecting the two proximal electrodes to a two channel Beckman

Dynograph. The dynograph was operated at a 25 mm./sec. paper speed and a 5 mv/cm deflection. A terminal board between the plants in the chamber and the recorder allowed the changing of hookup to experimental plants without rendering them insensitive.

The velocity of the action potential developed in all plants was determined by the following method. The time for conduction between pickup electrodes was obtained by measuring the distance, peak to peak, of the recorded impulse. This value was divided by the speed of the recording paper to obtain time in seconds. This time value was divided into the millimeter distance between pickup electrodes to obtain a velocity in mm./sec. For all experiments involving photoperiod, velocities were expressed in per cent of maximum daytime conduction velocity.

The effect of various stimulation voltages on impulse conduction was examined first. Plants were kept under a constant light, constant temperature condition, and the stimulus was varied by one volt intervals from 3 to 10 volts. This was done to find a threshold of stimulation and also to examine variability of conduction velocity at selected stimulus strengths.

In an attempt to show differences in conduction velocity at various times in the day-night period, plants were sampled initially with a varying day-night temperature of 29°C. day and 18°C. night. Conduction velocities were

obtained from nine plants. Each plant was sampled three times in each of the selected parts of the photoperiod. A thirty minute interval was allowed between stimulations to allow the plants recover. The times examined in the photoperiod were three hours after onset of light, at the onset of darkness and six hours after onset of darkness. The velocities were expressed as the per cent of maximum daytime conduction velocity. The data were examined by using a Student's t-test analysis of variance between the means of the selected groups (Li, 1964).

Plants were then sampled at a constant day-night temperature of 24°C. using the method described above. This data was also analyzed using Student's t-test.

An experiment was then conducted to show the degradation of the conduction velocity at selected times after the onset of darkness. Six plants were sampled in the light period and their maximum daytime values were recorded. These plants were then sampled from 5 to 30 minutes after onset of darkness at five minute intervals. Each plant was only used one time after darkness and the temperature was maintained at a constant value of 24°C. The conduction velocities for each time were recorded as the percent of daytime conduction. The data were subjected to linear regression analysis and a correlation coefficient was determined. The "t" values were then tested for significance at the 95% confidence level by using the formula $t = \frac{r\sqrt{n-2}}{\sqrt{1-r^2}}$ (Lewis, 1953).

DATA AND DISCUSSION

The general nature of the conducted impulse was studied with the aid of preliminary investigations and subsequent recordings of the biphasic impulse.

In TABLE I the nature of the impulse relative to stimulus strength indicates the variability of the impulse in the petiole of one plant.

TABLE I. Conduction velocities in the petiole of Mimosa as a function of DC voltage stimulus strength

	4V	5V	6V	7V	8V	9V	10V
Conduction Velocity in millimeters per second	0	12.7	13.5	13.3	12.6	13.0	12.1

This variability, about $\pm$ 5%, is probably due to the general variable nature of the conducted potential and is not necessarily a function of an increase in stimulus strength. A threshold value between 4 and 5 volts agrees with the work of Bose (1926) although methods were quite different. Conduction velocities shown in TABLE I have a mean velocity of approximately 12.9 mm./sec. This value falls within the range of velocities obtained by others using different modes of stimulation.

Biphasic potentials obtained at onset of darkness and during the daylight hours have potentials as shown in figures 1 and 2. In all plants tested immediately after the onset of

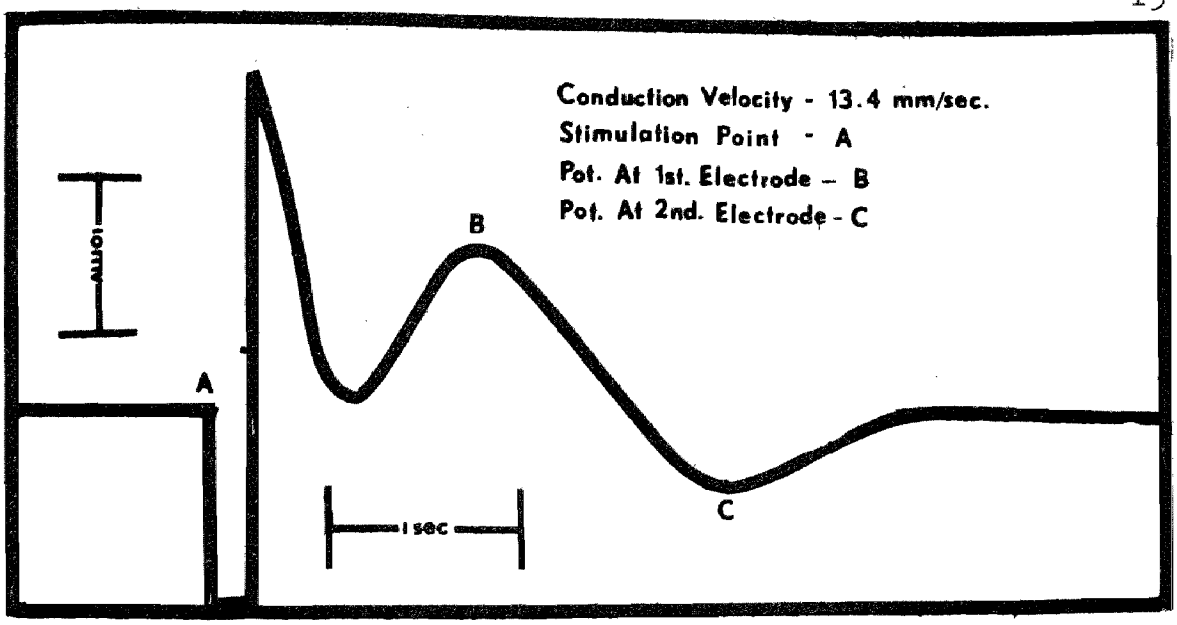

Fig. 1. Representative biphasic action potential developed in M. pudica petiole in light

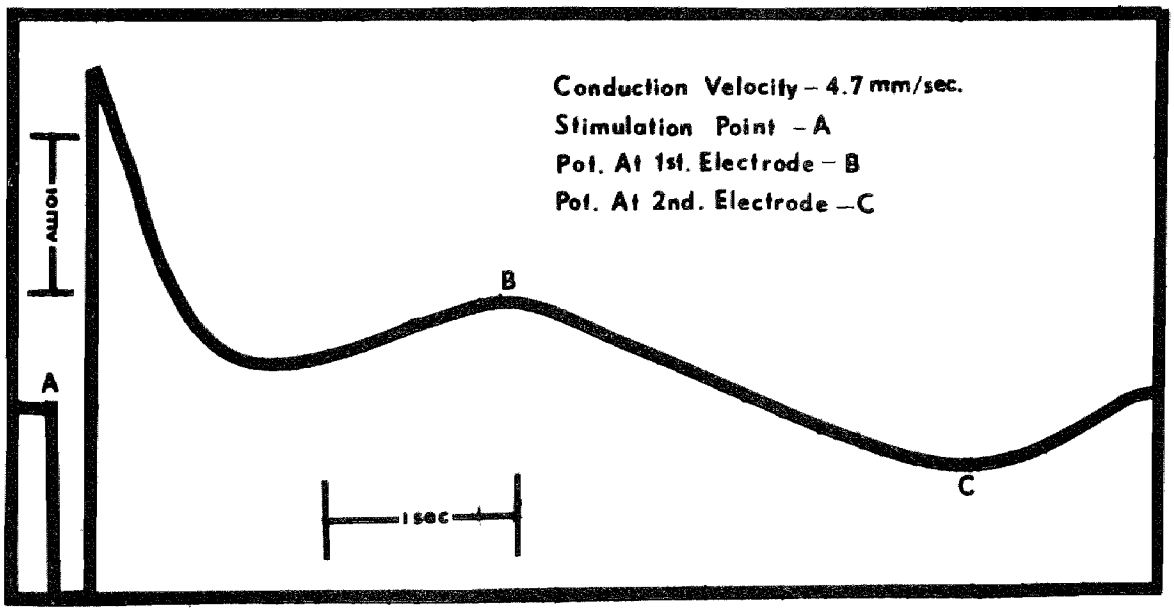

Fig. 2. Representative biphasic action potential developed in M. pudica petiole ten minutes after onset of darkness

darkness, there was a great decrease in the conduction velocity. The magnitudes of the action potential decreased slightly, perhaps because of variability of resistance in the electrodes. A reduction in velocity of approximately 60% is shown by comparing figure 1 with figure 2. Leaf drop at the primary pulvinus always occurred in light- and dark-treated plants even though the conduction velocity was much slower in the dark treatment.

Plants sampled at three times during the experiment with varying day-night temperature gave results in TABLE II.

TABLE II. Per cent of daytime conduction velocities at three selected times in the light dark period with a 29°C. day temperature and an 18°C. night temperature

	I 3 hrs. after onset of light	II 5 min. after onset of darkness	III middle of dark period
Number Sampled (n)	9	9	9
Mean velocity in per cent	87.66	20.44	6.11
Standard Deviation (S)	10.84	28.99	9.25

There is a great difference between means of the three groups and this could be caused by two factors. The reduction of the

velocity as has already been represented in figures 1 and 2 and the inability for some plants to recover in the dark periods at the 18°C. temperature value could be causing the low mean values. The effect of lowered temperature and the onset of darkness appeared to cause some plants to become insensitive and incapable of transmitting the action potential.

In applying Student's t-test to the data in TABLE II, significant difference is shown between light and dark samples while there appears to be no significance between the two dark sampled groups.

TABLE III. Student's t-test evaluating the significant difference of sample means in TABLE II

	Groups I-II	Groups I-III	Groups II-III
t value	6.1235	16.313	1.3468
Degrees of freedom	16	16	16
Percent significant difference of sample means	99+	99+	<90

Even though there was significance at the .01 level, it appears that temperature was having marked effects. The results of the experiment at a constant temperature of 24°C. is shown in TABLE IV. Conduction velocities in this run did not decrease as drastically as in the varying temperature

run and it appears as though there is an apparent recovery in the velocity as the plants are sampled well into the dark period. The reduction of the conduction velocity to approximately 50-60% of the daytime velocity appears to correlate with the initial tests and does show some correlation with results expressed later. The general variable nature of the impulse is again apparent as shown by the mean velocity of the impulse sampled during the day.

TABLE IV. Per cent of daytime conduction velocities at three selected times in the light-dark period with a constant temperature of 22°C.

	I 3 hrs. after onset of light	II 5 min. after onset of darkness	III middle of dark period
Number Sampled (n)	9	9	9
Mean Velocity in Per cent	91.77	58.0	76.1
Standard Deviation (s)	8.59	28.57	22.73

A variation of approximately ± 4% expressed in this table is very close to the variation shown earlier in TABLE I.

The data appearing in TABLE IV has been analyzed in TABLE V by application of Student's t-test.

TABLE V. Student's t-test evaluating the significant difference of sample means in TABLE IV

	Groups I-II	Groups I-III	Groups II-III
t value	3.1961	1.8347	1.4165
Degrees of freedom	16	16	16
Percent significant difference of sample means	99+	91	<90

Significant difference in conduction velocities is shown in groups I and II. The recovery of the ability of the petiole to transmit the impulse at daytime velocities is apparent since no significant difference is shown between groups I and III. The data in TABLE IV show that the ability of the petiole to conduct the stimulus dropped to a 58% value at onset of darkness; increasing to a 76% value later in the dark period.

The general nature of the loss of ability to conduct with the onset of darkness was tested by sampling the impulse every five minutes for a thirty minute period. The results are displayed in Figure 3. This loss closely approximates a linear regression which is expressed by the line $y = -1.56X-96.7$. The experimental values were tested for a linear regression and the correlation coefficient was .9957. The coefficient (r) of .9957 is quite exceptional and it was tested at the 95% confidence level.

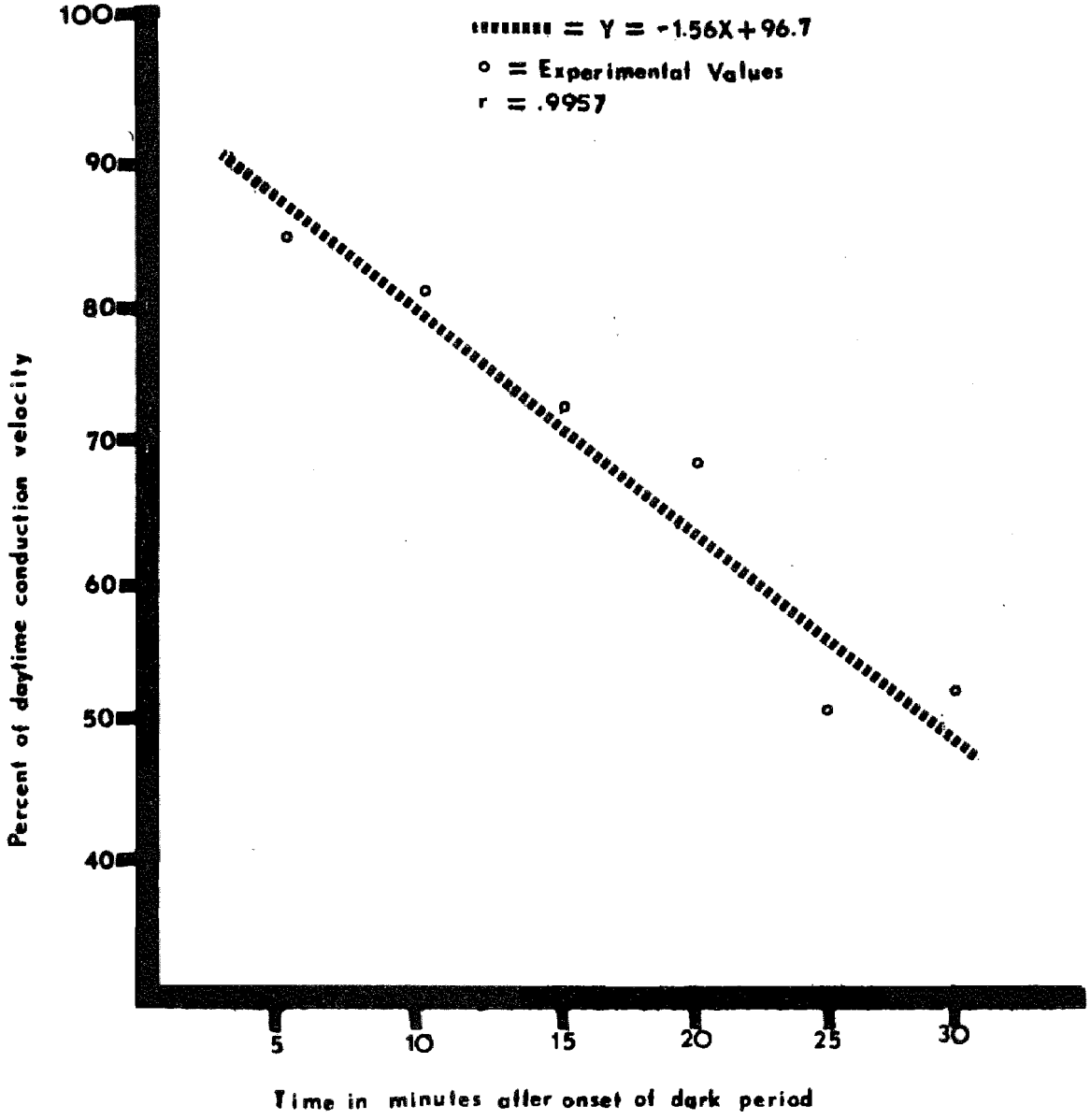

Fig. 3. Degradation of impulse conduction velocity in M. pudica petiole at selected times after onset of darkness

The calculated value of (r) at the 95% confidence level and four degrees of freedom was .81. Since the experimental coefficient exceeds the calculated coefficient at the .05 level the data are statistically significant.

CONCLUSION

M. pudica is capable of receiving electrical stimuli and generating action potentials which result in leaf drop. Many methods of stimulation are quite effective in causing leaf drop in M. pudica, but electrical stimulation is easily quantitied to a constant stimulation value. The method of pickup and recording of the impulse was quite effective and velocities in the petiole were found to substantiate the values found by Bose (1913b) and Sabaoka (1969). The general nature of the impulse recorded in this experiment agrees with the electrochemical method of conduction stated by Sibaoka (1953).

Temperature was found to affect the velocity of the impulse. Velocities of the impulse in the petiole increased directly as a function of temperature. This was also found by Bose (1926) in petiolar conduction and Wallace (1931) in pulvinar action. Impulse magnitudes also appeared to decrease slightly as temperature was lowered from 40°C.

Differential conduction velocities were found to exist in the acropetal and basipetal directions. Velocities were found to vary in the same manner described by Sibaoka (1969) with basipetal always slightly exceeding acropetal.

Certain new aspects of M. pudica conduction are revealed in this investigation. By sampling at various times in the photoperiod with a varying temperature, conduction velocities were found to be greatly reduced in the dark period. By using a constant day-night temperature, conduction velocities were found to be reduced but not to as great an extent. This was expected due to the temperature dependence of the impulse. By sampling at five minute intervals after onset of darkness, the reduction of the impulse velocity appears as a linear regression with a slope of -1.56. In all cases of impulse reduction there was also reduction in the magnitude of the action potential.

The reduction of impulse velocities in M. pudica at dark suggests the operation of some type of light sensitive pigment or system. It might be possible that phytochrome is the mechanism since it has been shown to effect other aspects of M. pudica sensitivity in much the same way. Fondeville (1966) showed that the night closing reaction of pinnule pairs occurred in about thirty minutes and that phytochrome was an enhancing agent.

As a result of this work and the work of others, new investigations could be conducted to extend our knowledge of M. pudica sensitivity. The action of phytochrome could be further investigated by observing the effects of red and far-red irradiation on the reduction of impulse conduction velocity.

Investigations to determine the mechanism developing electrochemical gradients could be the key to the understanding of many aspects of this movement in M. pudica.

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